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FOOD-RESOURCE PARTITIONING IN THE DEPOSIT FEEDING POLYCHAETE *PECTINARIA GOULDII*

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Although many benthic marine environments often support large populations of deposit feeding invertebrates, few studies have examined food-resource partitioning in this group of animals. Most studies dealing with different modes of feeding concentrate primarily upon the morphological characteristics of feeding structure (see Yonge, 1928). Sanders, Goudsmit, Mills and Hampson's (1962) study of the deposit feeders associated with the intertidal sand flats of Barnstable Harbor, Massachusetts, was one of the first attempts to categorize different types of material actually being ingested by detritovores. One of their major conclusions from the examination of the gut contents of 36 species of invertebrates was that most species exhibited generalistic feeding habits. Other studies (*e.g.*, Whitlatch, 1972) have shown some deposit feeders to be highly selective in their choice of particles.

The importance of deposit feeders in marine benthic communities is demonstrated by studies dealing with their effects on sediment stability and trophic structure (Rhoads and Young, 1970), distributions of other benthic organisms (Rhoads and Young, 1971) and water turbidity and nutrient recycling (Rhoads, 1973). Gordon (1966) has shown that *Pectinaria gouldii* (Verrill, 1873), a deposit feeding polychaete, has an annual sediment working rate of about 600 gm of sediment/worm. Using averages of 10 and 40 worms/m^2, he concluded that the sediment of one square meter and 6 cm deep could be completely reworked in 15 and 6 years, respectively. Because of the high rates of sediment working, this polychaete could have many effects upon the benthic environment. In the present study, *P. gouldii* was examined to ascertain feeding selectivity and the resultant effects upon the benthic community.

METHODS

Specimens of *P. gouldii* were collected at low tide from Little Sippewisset salt marsh, a shallow tidal enbayment located on the eastern shore of Buzzards Bay, north of Woods Hole, Cape Cod, Massachusetts (41°34′30″, 70°38′20″). The exact position of individual worms in the flat was determined by gently sliding a hand across the sediment; the tubes of the worms could easily be located in this manner. Twenty centimeter diameter cores were then taken and the sediment was removed with the worms in place. The sediment cores were brought to the laboratory and cooled at 4° C until time of dissection. The cores were vertically dissected (always within two hours of collection), and the worms were removed and immediately frozen. A sediment sample was taken at the level of the mouth and preserved in 70% alcohol.

The sediment sampled near the mouths of the worms was analyzed to determine particle size, percentage particle type abundance, and percentage organic material available to the organisms. Two subsamples of the sediment were stained with histological stains. Mercuric bromphenol blue was used for staining protein-containing material (Mazia, Brewer and Alfert, 1953). Humason (1967) states that this method appears to stain most proteins and peptides. Periodic acid Schiff reagent was used for staining carbohydrates. Humason (1967) mentions that this technique will stain a variety of substances including most protein-carbohydrate complexes. Sudan black B used for staining lipid material (Humason, 1967) was discontinued after preliminary staining of the sediment showed no reaction. The stained sediment was mounted on a slide and twenty random microscopic fields were recorded to determine the percentage of stained and unstained material. The particle size distribution of the samples was obtained by measuring the first 300 particles encountered on the slide.

Individuals of *P. gouldii* were removed from their tubes and sediment was collected from the foregut (as near the mouth as possible) and the intestine (after the digestive gland) with a modified Pasteur pipette. After the gut fractions were washed several times in distilled water to remove mucus, they were preserved in 70% alcohol. The procedures outlined above for the sediment fractions were employed to determine abundance of particle types and size distributions for these samples. The sediment and gut contents were examined at 200 × using a bright-field microscope with a calibrated eye-piece micrometer.

The results of the analysis of abundance of different particle types are expressed as percentage particle abundance. This measure is more important than volumetric and weight estimates in feeding studies since it reflects the relative amount of different types of particles an organism encounters while feeding. The measure, therefore, is valuable in determining food selection of different fractions of the environmental food-complex by the organisms.

The statistic used to determine feeding selectivity is described by Ivlev (1961) and is calculated as $E' = (r_i - p_i)/(r_i + p_i)$. For the ith food type, r_i equals the percentage ingested by the predator and p_i is the percentage of that food type available in the environment. The coefficient is finitely bounded and evenly distributed about zero. Zero indicates non-selective feeding; values from -1 to 0 indicate avoidance; and values of 0 to $+1$ indicate feeding preference.

Additional worms were brought to the laboratory for studies dealing with feeding habits. Fresh worms and sediment were collected and placed into 50 ml beakers. Observations of the feeding behavior were recorded using a vertically mounted dissecting microscope.

Results

Feeding habits

P. gouldii, which lives in a tapered tube composed of a single layer of large mineral grains, is normally positioned obliquely below the surface of the sediment. The head of the worm, located at the lower and larger end of the tube, is 1–5 cm

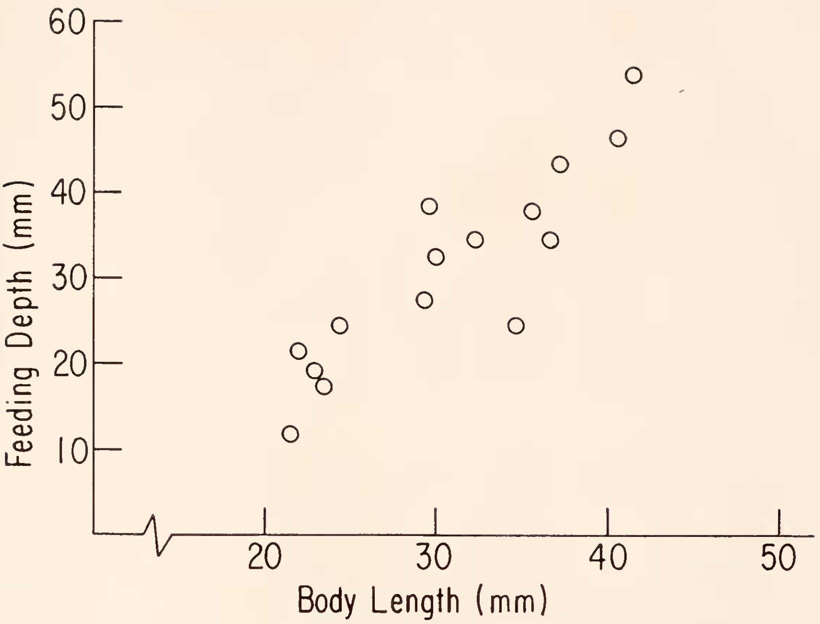

FIGURE 1. Relationship between body length of *Pectinaria gouldii* and depth of feeding.

below the surface. A highly significant relationship ($r = 0.90$, $P < 0.05$) exists between the length of *P. gouldii* and the depth at which the worm feeds (Fig. 1). Smaller individuals are found feeding closer to the surface than larger individuals.

P. gouldii has long golden paleae used strictly for digging and numerous long, ciliated, grooved tentacles which bring sediment to the mouth. When feeding, the tentacles independently select particles from all areas near the mouth. The selected particles are brought to the mouth and rejected particles fall to the bottom of a feeding cavern which the worm creates while feeding. The selected sediment is either ingested or transported between the worm's body and tube to the surface of the flat where it is deposited around the posterior end of the tube. As the worm slowly moves through the sediment, the small excavated cavity continually collapses and fills in with sediment from the sides. Previous ecological studies on the genus *Pectinaria* include Gordon's (1966) work on the sediment reworking activities of *P. gouldii* and Waston's (1927) description of the natural history of *P. koreni*, a European species.

Particle composition of the environmental food-complex

The particle composition of the sediment obtained near the mouths of fifteen specimens of *P. gouldii* is presented in Table I. The classification of different possible food sources available to the polychaete are as follows: (a) *Encrusted minerals*—mineral grains encrusted with living matter, organic debris, or other encrustations. Encrusted material was determined by visual observations. Steele and Baird (1968) have found that nearly all of the organic component in a sandy

TABLE I

Per cent particle type abundance of sediment sampled near the mouth of Pectinaria gouldii

Particle type	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
Mineral $>75\ \mu$ encrusted	3.8	6.3	13.4	13.2	9.2	7.5	7.7	1.3	3.7	0.6	0.9	5.9	4.4	6.7	7.0
Mineral $>75\ \mu$ not encrusted	5.6	8.7	28.9	16.0	12.3	5.6	13.5	2.1	1.8	1.4	2.3	9.8	6.7	9.4	13.9
Mineral 25–75 μ encrusted	0.0	0.0	0.5	0.0	0.8	0.0	0.0	0.3	0.5	0.2	0.1	0.4	0.2	0.1	0.4
Mineral 25–75 μ not encrusted	9.3	10.8	6.7	8.3	7.9	7.6	8.6	6.2	7.4	5.7	6.1	14.0	12.4	9.7	10.1
Mineral $<25\ \mu$	44.6	41.9	32.5	44.1	41.9	53.4	50.4	52.5	50.7	53.9	49.9	46.2	45.8	49.7	41.9
Floc aggregates	31.5	27.0	16.6	14.0	19.3	21.3	15.9	30.2	32.8	33.3	31.5	18.8	25.7	19.5	22.4
Fecal fragments	3.0	3.2	1.1	1.8	0.6	2.9	2.3	2.2	1.7	1.8	3.9	3.7	3.3	0.8	2.5
Plant fragments	0.9	0.7	0.0	0.3	0.4	0.5	0.0	0.5	0.2	0.6	0.7	0.3	0.5	0.5	0.8
Dead diatoms	0.8	0.8	0.3	1.8	0.8	0.9	1.5	2.5	0.3	1.7	2.7	0.4	0.4	1.0	0.9
Others	0.5	0.6	0.0	0.5	1.6	0.3	0.1	2.2	0.9	0.8	1.9	0.5	0.6	2.6	0.1

beach existed as encrustations upon sand grains. This includes bacteria and other micro-organisms described by Anderson and Meadows (1969) and Batoosingh and Anthony (1971). It seems likely, therefore, that encrusted mineral grains could be an important food source for deposit feeding organisms. (*b*) *Fecal material*—fecal pellets and fragments found in the sediment. The importance of fecal material as a food source for invertebrates has been demonstrated by Newell (1965) and Johannes and Satomi (1966). (c) *Floc aggregates*—amorphous material consisting primarily of organic and inorganic debris. The origins of this material may be from both plant and animal sources and is usually referred to as detritus. Considerable research has been directed in defining detritus as a food stuff (Darnell, 1967; Fox, 1950; Odum and de la Cruz, 1967; Adams and Angelovic, 1970). (d) *Plant fragments*—dead and decomposing plant material. Odum and de la Cruz (1967) have shown that decomposing plant material is actually a better food source than living tissue.

The composition of the different particle types associated with the sediment is quite consistent between samples (Table I). Mineral grains less than 25 μ are the most abundant particle type. Mineral grains and floc aggregates comprise more than 90% of the total sediment.

Feeding selectivity

From his study of sediment working of *P. gouldii* collected from Barnstable Harbor, Gordon (1966) concluded that the polychaete was a non-selective deposit feeder and did not sort particles for ingestion according to size. His conclusions were based upon comparisons of particle size distributions in the gut to that of sediment collected on the surface of the sand flat where the worms were feeding. Gordon failed, however, to note the length of individual worms or sample the sediment that the worms were directly feeding upon.

In the present study, *P. gouldii* is found to be selectively feeding upon the sediment at Little Sippewisset salt marsh. Figure 2 shows that larger worms are selecting, on the average, larger particles than smaller worms ($r = 0.85$, $P < 0.05$). This may be the result of two factors. Smaller individuals of *P. gouldii* feed closer to the surface than larger individuals. Since the average

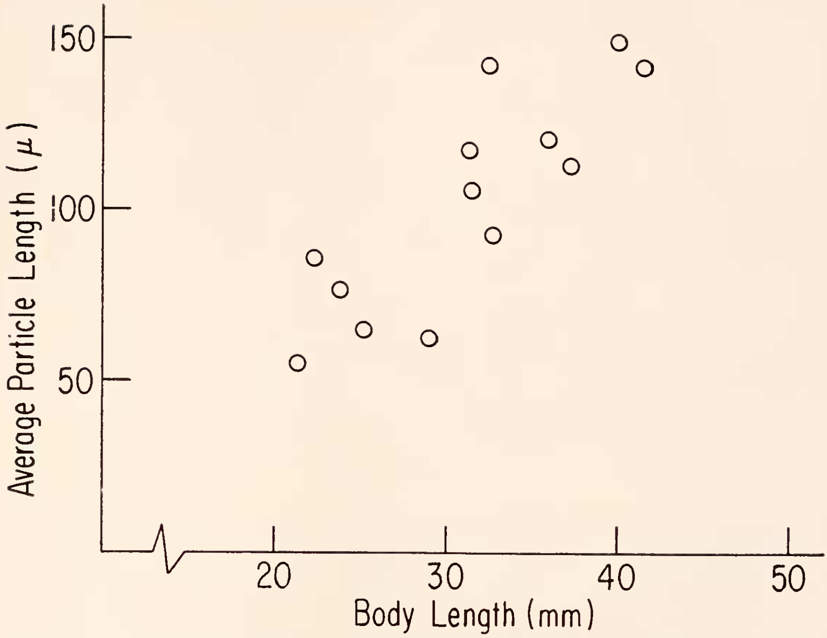

FIGURE 2. Relationship between body length of *Pectinaria gouldii* and length of average-sized particle ingested by the polychaete.

particle size of the sediment increases slightly with depth, the animals may be feeding in completely different sedimentary environments. Secondly, the size selection may be the result of a morphological constraint placed upon the organisms (*e.g.*, mouth size, ability of the feeding tentacles to obtain particles, *etc.*) that changes with size (age) of the polychaete.

Feeding selectivity coefficients are presented in Figure 3 for the six most abundant particle types found in the foregut (more than 95% of the particles

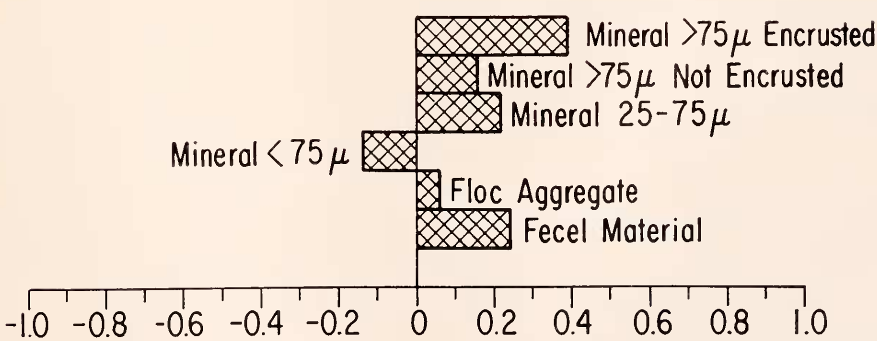

FIGURE 3. Electivity coefficients of different particle types selected by *Pectinaria gouldii* (data averaged for fifteen worms).

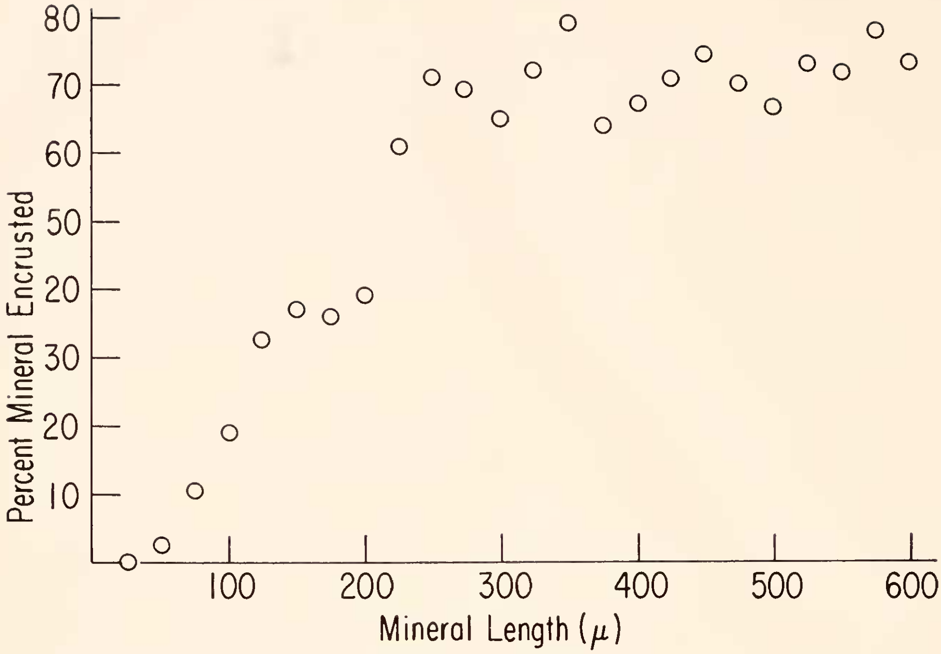

FIGURE 4. Relationship between mineral length found in the sediment where *Pectinaria gouldii* is feeding and percentages of minerals having encrustations. Mineral lengths are clumped into 25 μ size groups.

ingested). The data indicate that *P. gouldii* consistently prefers large encrusted mineral grains greater than 75 μ. Nonencrusted mineral grains greater than 75 μ and encrusted mineral 25–75 μ show positive electivity values in most of the worms. Fecal material and floc aggregates were selected in the majority of animals, though fecal material was selected more often. In all the polychaetes studied, there was avoidance (probably due to a mechanical or morphological constraint) for mineral grains less than 25 μ.

The percentage of encrusting material on the mineral grains is highly correlated with grain size (Fig. 4). Mineral grains less than 25 μ are never encrusted while grains greater than 75 μ are increasingly encrusted (10–80%). *P. gouldii* may be preferentially selecting large grains to increase the amount of organic matter ingested. As already noted, fecal material and floc aggregates are highly important food sources for deposit feeders and may be selected for the same reason.

Sediment staining

Table II gives the results of the periodic acid Schiff (PAS) staining of the sediment near the mouth, sediment ingested and sediment sampled from the intestine of *P. gouldii*. Analysis of the sediment samples near the mouth of the worms indicates an average of 32.7% of the particles are possible sources of organic matter. Possible sources of organic matter refers to the total material that could be regarded as a food source (as outlined above) for the polychaetes. The total

PAS stained material averages 13.9%. Of the 32.7% possible organic material, less than half (average of 42.6%) was stained by the carbohydrate stain suggesting that not all of the material is organic in nature. Studies by Waksman and Hotchkiss (1937), Anderson (1940), Mare (1942) and George (1964) have strongly suggested that only about 10–20% (by weight) of the organic matter in marine sediments is in a biologically utilizable form.

Analysis of the sediment from the foregut of the worms shows an average of 42.7% possible organic matter of which 20.5% was PAS stained. There was an average of 30.9% possible organic material obtained from the intestine of the worms of which 14.3% stained by the PAS method.

The mercuric bromphenol blue (MBB) method stained only a very small amount of material in the sediment. Of four samples analyzed, less than 0.4% of the material showed MBB reactions. Less than 0.1% of the ingested fraction obtained from the foregut of the worms stained with the MBB method, while sediment sampled from the intestine showed no reaction to this stain.

Discussion

Calculations of the assimilation efficiency of *P. gouldii* show that the worms remove on the average 30% of the possible organic material from ingested sediment. Assimilation efficiencies of PAS-stained sediment average 29.1% for the fifteen worms. Gordon (1966) reports that *P. gouldii* removed almost 50% of the organic material (by weight) from each gram of sediment worked. George (1964) states that the deposit feeding polychaete *Cirriformia tentaculata* removes only 7.9% (by weight) of the organic matter present in the sediment. Adams and Angelovic (1970) found that the polychaete *Glycera dibranchiata* has an assimilation rate of 41% (based upon the amount of ^{14}C respired as CO_2) when fed detritus and 34% when fed undecomposed eel grass. Since the values presented in this study are not volumetric or by weight it is difficult to make comparisons with assimilation rates presented in the other studies. However, the values presented are well within the range of the other studies on assimilation efficiences.

Table II

Per cent particle abundance of carbohydrate staining (periodic acid Schiff)

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
Sediment near mouth of *P. gouldii*															
Per cent "possible" organic	38.9	37.3	31.1	33.1	32.4	31.2	25.9	30.8	32.1	36.5	33.3	29.1	36.5	29.4	33.0
Per cent stained	10.2	5.9	13.1	14.0	13.7	12.4	9.4	11.5	15.7	16.5	18.2	18.6	17.6	13.8	18.6
Per cent organic stained	26.2	15.8	42.1	42.3	42.3	39.7	36.3	37.3	48.9	45.2	54.6	63.9	48.2	46.9	56.4
Sediment in foregut of *P. gouldii*															
Per cent "possible" organic	41.9	37.9	48.1	45.7	36.5	43.3	53.9	41.6	46.1	40.1	47.3	42.2	43.5	36.2	36.9
Per cent stained	18.6	17.9	21.9	16.5	13.9	18.6	18.2	23.9	31.4	24.5	28.1	13.3	23.4	21.3	15.4
Per cent organic stained	44.4	47.2	45.5	36.1	38.1	42.9	33.8	57.5	61.2	61.1	59.4	31.5	53.8	58.8	41.7
Sediment in hindgut of *P. gouldii*															
Per cent "possible" organic	28.1	28.3	33.2	33.3	28.4	31.4	37.2	32.5	40.1	33.5	29.5	26.1	22.7	28.2	31.2
Per cent stained	12.9	13.1	16.1	11.7	11.4	8.9	17.0	17.2	27.0	17.9	13.5	11.7	15.3	10.0	11.4
Per cent organic stained	45.9	46.3	48.5	35.1	40.1	28.3	45.7	52.7	68.1	53.4	45.8	44.8	67.6	35.5	36.5
% "Possible" assimilated	33.2	25.3	30.9	27.3	22.2	27.5	30.9	21.9	13.0	16.4	37.6	38.1	47.8	22.1	15.4
% Stained assimilated	30.6	26.8	26.5	29.1	17.9	52.2	6.6	28.0	14.0	26.9	51.9	12.0	34.6	53.1	25.9

Data presented in this study provide some interesting results concerning the possible effects of the polychaete on the benthic environment. The worms concentrate an average of 32.7% possible organic material found in the sediment to 42.7% by selectively feeding. Through the concentration of organic material, the animals are channeling large amounts of organic material to the surface where it can become available to other organisms. The feeding activities of *P. gouldii* could have important effects upon the recycling of nutrients for the salt marsh tropic chain. The organic fraction deposited upon the surface may even be suspended in the water column. Rhoads (1973), for example, has shown that resuspended fecal material of benthic deposit feeders in Long Island Sound may represent a significant food source for commercially important suspension feeding molluscs.

The use of histological staining techniques for examination of sediments is a biologically meaningful way to ascertain the qualitative and quantitative composition of marine sediments. The staining methods, although very generalized in their staining affinities, are valuable in determining the nature of the food sources for benthic animals and those portions that may be biologically utilizable.

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Summary

1. A study of the food-resource partitioning in the deposit-feeding polychaete *Pectinaria gouldii* collected from Little Sippewisset salt marsh, Massachusetts, shows that, on the average, larger worms select larger particles than smaller worms. Comparisons of ingested sediment with sediment collected where the animals were feeding indicate that the polychaetes prefer organic-encrusted mineral grains, floc aggregates, and fecal material.

2. Histological stains were used to determine the percentage particle abundance of different possible food sources and fractions ingested by the polychaetes. Mercuric bromphenol blue (MBB) was used to stain protein-containing material and periodic acid Schiff reagent (PAS) was used to stain carbohydrate-protein complexes. Total possible organic material in the sediment averaged 32.7%. Very little of the sediment (less than 0.4%) stained with MBB, while an average of 13.9% of the sediment stained with PAS. Of the total possible organic matter, only about one-half stained with the PAS reagent suggesting not all of the material is organic in nature.

3. Analysis of the sediment ingested by the worms averaged 42.7% possible organic matter, of which 20.5% was PAS-stained. Calculations of the assimilation efficiencies of *P. gouldii* show that the worms remove, on the average 30% of the possible organic matter and 29.1% of the stained material from the sediment.

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